Genotype — Environment Interactions in Growth of Chum Salmon

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GENOTYPE - ENVIRONMENT INTERACTIONS IN GROWTH OF CHUM SALMON

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ABSTRACT

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Weights of five full-sib families of chum salmon (Oncorhynchus keta) were monitored in a higher temperature fresh water environment and lower temperature salt water environment for 196 days after fry emergence. Chum salmon grew more rapidly in the higher temperature fresh water environment than in the lower temperature salt water one. Heritability of weight was higher in higher temperature fresh water than in lower temperature salt water, and there was a significant genotype - environment interaction for body weight. Families ranked differently with respect to weight and instantaneous growth rate in the two environments. Strains adapted to specific environmental conditions may be desirable in enhancing growth rates.

RESUME

Beacham, T. D. 1987. Genotype - environment interactions in growth of chum salmon. Can. Tech. Rep. Fish. Aquat. Sci. 1517: 11 p.

Pendant 196 jours après l'émergence des alevins, l'auteur a suivi la variation du poids chez cinq familles apparentées de saumon kéta (Oncorhynchus keta) vivant en eau douce à température élevée et en eau salée plus froide. La croissance du saumon kéta s'est effectuée plus rapidement dans le premier environment que dans le second. Le caractère héréditaire du poids était plus prononcé en eau douce à température élevée; de plus, il existait une nette interaction génotype-envirnnement pour ce qui est du poids corporel. Le classement des familles variait selon le poids et le taux instantané de croissance dans les deux environnements. Les souches adaptées à des conditions environnementales particulières peuvent être avantageuses pour ce qui est de l'augmentation des taux de croissance.

INTRODUCTION

The development of strains of Pacific salmon suited to aquaculture both in marine and fresh water environments depends on assessing the relative magnitude of genetic, environmental, and genotype - environment interaction sources of variation for economically important traits. Research on genetic variation for a number of salmonid traits has been conducted, with alevin hatching time (McIntyre and Blanc 1973; Sato 1980), embryo and alevin survival (Kanis et al. 1976; Gall and Gross 1978a; Robison and Luempert 1984), and juvenile growth and survival investigated (Aulstad et al. 1972; Ayles 1975; Refstie 1980; Gunnes and Gjedrem 1981). The effect of environmental variation on these traits has been investigated for an extensive period of time (Hayes et al. 1953; Brett et al. 1969; Timoshina 1972; Gunnes 1979), but interactions between genotypes and specific environmental factors have only recently been examined quantitatively for salmonid growth. McKay et al. (1984) reported that growth rates of rainbow trout (Salmo gairdneri) families relative to each other was dependent upon the rearing temperature, and thus strains adapted to local environmental conditions should be considered for aquaculture.

In British Columbia, chum salmon (Oncorhynchus keta) have a diverse life history, spawning in a variety of habitats during a prolonged spawning season. However, in most stocks, the fry migrate directly to the ocean after emergence from the redds in the spring, although some fresh water feeding and growth has been documented (Sparrow 1968; Beacham and Starr 1982). Interest is developing in fresh water aquaculture of Pacific salmon, but selective breeding programs will likely concentrate on producing strains with enhanced marine growth and survival. The present study was conducted to compare the relative growth rates of genotypes in marine and fresh water environments.

MATERIALS AND METHODS

Gametes were collected from five male and five female spawning chum salmon on January 10, 1984 from the Chemainus River on the southeast coast of Vancouver Island. Sperm from a single male fertilized the eggs of a single female, producing five full-sib families, and the fertilized water-hardened eggs were loaded into a vertical stack incubator with an incubation temperature of 4°C. Thirty eggs per female were preserved in 10% formalin for subsequent determination of egg weight. Once hatching began, the number of alevins was recorded daily, and within one day of 50% hatching, 30 alevins per family were preserved in 10% formalin for subsequent determination of alevin weight. Fry emergence or swim-up occurred on July 7-9, 1984, at which time 30 fry per family were preserved for determination of fry weight.

At swim-up, fry from each family were distributed to four separate 35-L tanks, two supplied with ambient dechlorinated tapwater and two with ambient seawater at a flow rate of 4 L/min. The fry from the five families were thus distributed into 20 tanks (10 fresh water, 10 salt water). Loading densities were 50 fry/tank, except for family 5, where only 35 fry/tank were available. The fish were exposed to artificial lighting that approximated the natural photoperiod regime. They were fed Oregon moist pellets (OMP) daily to satiation using automatic feeders. After 77 days of rearing, the fish from each family were anesthetized with MS 222, weighed to the nearest tenth of a gram, marked as to family and then transferred to a 2400-L tank supplied with either ambient fresh or salt water at a flow rate of 32 L/min. All families in each environment (fresh or salt water) were thus subsequently reared in the same tank. Lighting and feeding regimes were maintained as previously indicated. Families were identified through a combination of a maxillary clip and adipose and pelvic fin clips. After 142 days of rearing, all salmon in both the fresh and salt water tank were anesthetized, identified to family, and then weighed to the nearest tenth of a gram. A severe outbreak of furunculosis (caused by Aeromonas salmonicida) occurred in the salmon reared in salt water subsequent to the 142 day sampling period. The experiment was consequently terminated after 196 days of rearing with 196-day weights of salmon reared in fresh water only recorded. Water temperatures in both the ambient fresh and salt water supplies were recorded daily and the mean weekly average temperature in each environment is outlined in Figure 1.

Variation in weight after 77 days of rearing was investigated with the model:

$$Y_{ijkl} = \mu + F_i + E_j + FE_{ij} + R_{ijk} + e_{ijkl}$$

where Y_{ijkl} = observed weight
μ = overall mean
F_i = effect of family (i = 1,5)
E_j = effect of environment (j = 1,2)
FE_{ij} = family - environment interaction
R_{ijk} = effect of tanks within families and environment (k = 1,2)
e_{ijkl} = error term for l'th observation in subgroup ijk

The environment effect was considered fixed, with other effects random. Variance components for families and the residual were calculated with the model (environments separate):

$$Y_{ij} = \mu + F_i + e_{ij}$$

with the terms defined as previously noted. Heritability of body weight was determined in each environment separately as outlined by Becker (1984):

$$h^2 = \frac{2\,\sigma_s^2}{\sigma_s^2 + \sigma_w^2}$$

where σ_s^2 = family variance component

σ_w^2 = residual variance

The standard error of the estimate of heritability was determined by the method outlined by Becker (1984). The genetic correlation between family weights in fresh and salt water was determined by the method for mixed models as outlined by Yamada (1962). Instantaneous growth rates were calculated as outlined by Krebs (1978). Ranking of the families in both environments was compared with a Spearman rank correlation coefficient (Mendenhall 1971). Variation in weight after 142 days of rearing was analysed with the model:

$$Y_{ijk} = \mu + F_i + E_j + FE_{ij} + e_{ijk}$$

with the terms defined as in the model used for the analysis of the 77-day weights. Tank effect was now included with the environmental variance component.

RESULTS

GROWTH RATES

Initial egg weight had a marked effect both on alevin weight at hatching ($r=0.91$, $n=5$, $P<0.05$) and fry weight at emergence ($r=0.96$, $n=5$, $P<0.01$) (Table 1). After 77 days of rearing, egg size was no longer related to subsequent fish size in either the fresh water ($r=-0.74$, $P>0.10$) or salt water environments ($r=-0.58$, $P>0.10$). In fresh water, there were significant differences among families ($F_{4,5} = 8.93$, $P<0.05$) and between tanks within families ($F_{5,279} = 6.86$, $P<0.05$) for 77-day weight of salmon. In salt water, there were also significant differences in weight among families ($F_{4,4} = 23.38$, $P<0.05$) but not between tanks ($F_{4,284} = 0.56$, $P>0.10$). There were marked differences in fish weight between the two environments, with the salmon reared entirely in freshwater approximately twice as heavy as those reared in salt water ($F_{1,4} = 37.52$, $P<0.01$) (Table 1). The mean fresh water temperature during this period was 17.8°C, while the mean salt water temperature was 11.5°C. There was a significant family - environment interaction ($F_{4,9} = 5.31$, $P<0.05$), which indicates that families in the two environments for body weight did not grow in the same relative manner. This was also indicated by the lack of association among the ranks of the families in the two environments for body weight (rank correlation coefficient $r_s = 0.45$, $P>0.10$) or instantaneous growth rate ($r_s = 0.80$, $P>0.10$). The rearing environment clearly had a marked effect on both the absolute and relative body weight of salmon after 77 days of rearing.

The rearing environment continued to have a significant effect on body weight 142 days after fry emergence. There were significant differences among families in body weight in both fresh water ($F_{4,248} = 57.56$, $P<0.01$) and salt water ($F_{4,276} = 19.64$, $P<0.01$). Chum salmon reared in fresh water remained about twice as heavy as those reared in salt water ($F_{1,4} = 62.32$, $P<0.01$), and a significant family - environment interaction remained ($F_{4,524} = 20.13$, $P<0.01$). No association was evident in the rankings of body weights of the families in the two environments ($r_s = 0.10$, $P>0.10$) or in the instantaneous growth rates between 77 and 142 days ($r_s = 0.30$, $P>0.10$).

After 196 days of rearing, there were significant differences in mean body weight among families reared in fresh water ($F_{4,216} = 61.26$, $P<0.01$), with family 3 significantly larger than the other four families (Table 1). The relative rankings of the families reared in fresh water changed among the 77, 142, and 196 day sampling periods, and thus the timing of evaluation of growth performance of the families is important in any selective breeding program. The investigation was terminated after 196 days due to the nearly 100% mortality rate (due to furunculosis) of salmon reared in salt water prior to the sampling period.

HERITABILITY OF WEIGHT

The variance component σ_s^2 estimates 1/2 of the additive genetic variance, 1/4 of the dominance variance, and various amounts of the epistatic variance, and σ_e^2 estimates the remainder of the genetic variance plus the environmental variance (Becker 1984). Nonadditive genetic variance is included in this estimate of heritability, and Aulstad et al. (1972) indicated that the intraclass correlation for full-sib groups can be used as an upper limit for the genetic influence of a trait. Estimated variance components and intraclass correlation were larger for those chum salmon families reared in fresh water as compared to those reared in salt water (Table 2). Heritabilities of body weight based upon a full-sib mating design were higher for the salmon reared in fresh water than those reared in salt water (Table 3). In each environment, heritabilities increased over time. The genetic correlation between body weight in fresh and salt water was less than 1.0 and declined with time, indicative of an increasing genotype - environment interaction.

DISCUSSION

Chum salmon in the fresh and salt water environments had remarkably different growth responses, with salmon in fresh water having higher growth rates and higher heritability of body weight than did those in salt water.

Salinity obviously varied between the two environments, but there was also a significant temperature difference, with fresh water being warmer than salt water until two weeks before the second sampling period. Differences in salmon growth rates between the two environments may thus be attributable to either salinity or temperature differences. However, when the same temperatures are compared, early growth rates of chum salmon are similar in fresh water and in salt water (Shelbourn 1980), and thus salinity differences between the two environments are unlikely to result in differential growth rates. The higher growth rates of chum salmon in fresh water were probably due largely to the warmer water temperatures that they experienced relative to salt water, with chum salmon having faster growth rates in increasing water temperatures up to at least 15°C (Shelbourn 1980).

Heritabilities of body weight in juvenile salmonids indicate that significant genetic variation for this trait is present in many species. Full-sib heritabilities for rainbow trout weight up to two years of age ranged from 0.32 to 1.04 (Gall 1974; Gall and Gross 1978b; Klupp 1979). Heritability of weight (sire components) for rainbow trout at 150 days was 0.17, at 280 days 0.32 (Aulstad et al. 1972), and at one year 0.38 (Linder et al. 1983) or 0.20 (McKay et al. 1986). Robison and Luempert (1984) reported a sire component of heritability for brook trout (Salvelinus fontinalis) 35 days (0.08) and 134 days (0.60) after first feeding, with the dam component heritability recorded as 0.34 and 0.37, respectively. The relatively high heritability for body weight for salmon in my study suggests that selection for rapid growth should be successful, and if there is a high genetic correlation between body weight at 196 d and adult weight, then selection for potential brood stock could occur early in the life cycle.

In my study, heritability estimates and evidence for genotype-environment interactions are based on five full-sib families. The small number of families and the breeding design used do not allow precise estimates of either heritability of juvenile weight or the convincing demonstration of a genotype-environment interaction. However, even with these limitations, no other comparable information is available for chum salmon.

Heritability estimates derived from full-sib matings include both components of the additive and non-additive genetic variance, and maternal effects such as egg size and cytoplasmic inheritance. As the heritability estimates include maternal effects, estimates of heritability of weight should be derived from a half-sib or factorial breeding design if the intention is to provide information for selective breeding programs. Probably at least 20 families should be examined in future in genotype-environment interactions in chum salmon growth rates.

Genotype - environment interactions can be detected by a low genetic correlation between the same trait in different environments (Falconer 1952). Genotype - environment interactions for salmonid growth rates have been reported by Ayles (1975), Klupp et al. (1978), Gunnes and Gjedrem (1981), and McKay et al. (1984), which indicates that the environment can have a differential effect on specific genotypes. The genotype - environment interaction for chum salmon growth rate indicated in my study is probably indicative of differential growth rates of genotypes with respect to water temperature. Fresh water temperatures ranged from 16 to 20°C (mean 18°C) to the first weighing period at 77 days. This high temperature was probably

above the temperature for optimum growth, and the observed genotype - environment interaction may be indicative of differential suitability of families to high water temperatures. Strains adapted to specific environmental conditions should be considered in developing a breeding program.

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Table 1. Mean egg weight (mg), alevin weight (mg), fry weight (mg), and fish weight (g) 77, 142, and 196 days after swim-up for five full-sib chum salmon families reared in fresh and salt water. Standard errors are in parentheses. Sample size is indicated below mean.

Stage	Family 1	2	3	4	5
			Fresh water		
Egg	271.6 (2.19) 30	277.0 (1.82) 30	217.5 (0.76) 30	271.5 (1.85) 30	218.2 (1.44) 30
Alevin	250.0 (2.78) 29	262.4 (3.78) 30	223.5 (1.84) 30	274.0 (3.93) 30	218.1 (2.31) 30
Fry	356.5 (1.91) 30	378.2 (2.54) 30	321.8 (1.51) 30	377.0 (2.56) 30	313.5 (2.80) 30
77 day	11.40(0.38) 36	8.26(0.16) 77	11.11(0.20) 68	7.58(0.30) 74	13.35(0.76) 34
142 day	37.56(1.01) 32	37.59(0.64) 69	49.78(0.77) 65	33.86(0.88) 64	38.47(1.68) 23
196 day	51.14(1.51) 26	53.55(0.91) 64	70.97(0.94) 54	50.97(1.11) 58	52.75(2.11) 19
			Salt water		
77 day	5.01(0.11) 94	3.71(0.16) 50	5.48(0.23) 57	4.29(0.14) 50	4.52(0.23) 42
142 day	21.35(0.44) 92	18.23(0.43) 47	25.68(0.71) 55	22.12(0.59) 48	21.25(0.75) 39

Table 2. Estimated variance components for families (σ_s^2) and residual (σ_e^2) and intraclass correlation (t) for body weight.

Environment	Age (d)	σ_s^2	σ_e^2	t
Fresh water	77	5.34	5.22	0.51
	142	46.67	40.26	0.54
	196	84.99	59.72	0.59
Salt water	77	0.39	1.66	0.19
	142	6.33	18.58	0.25

Table 3. Heritability estimates (and standard error) of body weight and genetic correlation between body weight in fresh and salt water for five chum salmon families reared in fresh and salt water for 77, 142, and 196 days after fry swim-up.

Period (days)	Heritability		Genetic correlation
	Fresh	Salt	
77	1.01 (0.36)	0.38 (0.24)	0.86
142	1.07 (0.36)	0.51 (0.28)	0.75
196	1.17 (0.18)		

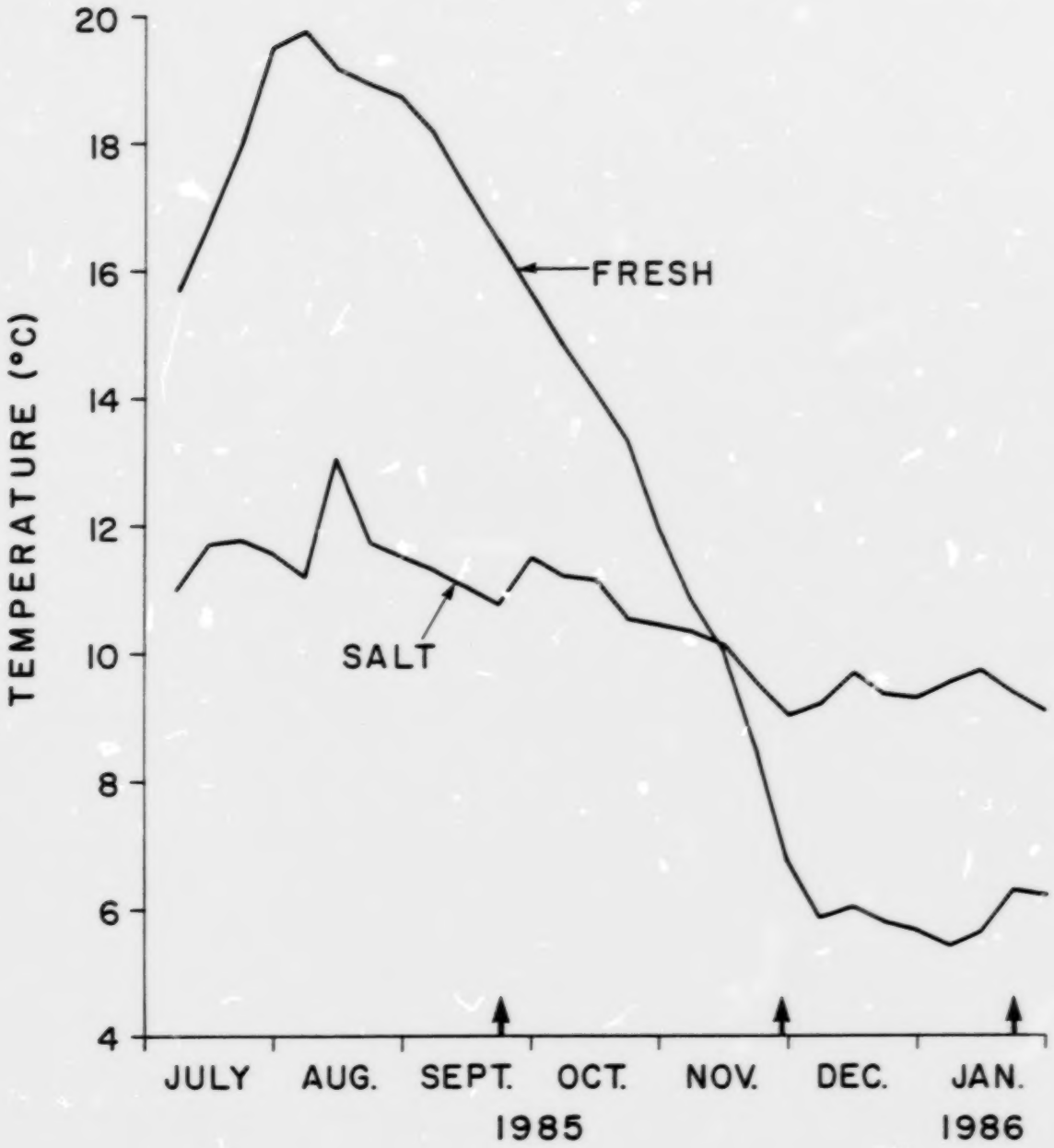

Fig. 1. Mean weekly water temperatures for fresh and salt water. Arrows indicate timing of first, second, and third sampling periods.